HILL CANE (ARUNDINARIA APPALACHIANA), A NEW SPECIES OF BAMBOO (POACEAE: BAMBUSOIDEAE) FROM THE SOUTHERN APPALACHIAN MOUNTAINS J.K.Triplett¹ A.S.Weakley

Department of Ecology, Evolution and Organismal Biology Iowa State University Ames, Iowa, 50011-1020, U.S.A. Univ. of North Carolina Herbarium (NCU) North Carolina Botanical Garden University of North Carolina Campus Box 3280 Chapel Hill, North Carolina, 27599-3280, U.S.A.

L.G. Clark

Department of Ecology, Evolution and Organismal Biology Iowa State University Ames, Iowa, 50011-1020, U.S.A.

ABSTRACT

A newly recognized species of *Arundinaria* from the southern Appalachian Mountains is described, illustrated, and compared with the related species *A.gigantea* and *A.tecta*. **Arundinaria appalachiana** is distinguished by a combination of vegetative morphological characters including features of branching and leaf morphology, leaf anatomy, and ecology. Recognition of this species is consistent with genetic data that provide evidence for monophyly of the species and its sister relationship with *A.tecta*. A key for the identification of *Arundinaria* species in North America is included along with a comparative table based on morphology, leaf anatomy, and ecology.

KEY WORDS: bamboo, Arundinaria, eastern U.S., Appalachian Mountains

RESUMEN

Se describe e ilustra una nueva especie de *Arundinaria* del sur de la Cordillera de los Apalaches y se la compara con las especies relacionadas *A.gigantea* y *A.tecta*. Se distingue **Arundinaria appalachiana** por una combinación de caracteres morfológicos vegetativos, entre ellos aspectos de la ramificación, morfología y anatomía de las hojas, y ecología. El reconocimiento de esta especie concuerda con datos genéticos que apoyan la monofilia de la especie nueva y su posición como especie hermana a *A.tecta*. Se incluye una clave para la identificación de especies de *Arundinaria* en América del Norte y una tabla comparativa basada en la morfología, anatomía de las hojas, y ecología.

PALABRAS CLAVES: bambú, Arundinaria, este de los Estados Unidos, la Cordillera Appalachiana

INTRODUCTION

Arundinaria Michx. is a genus of north temperate woody bamboos (Poaceae: Bambusoideae) with a complex taxonomic history involving numerous entities that have been placed within it at one time or another over the past two

¹Author for correspondence (triplett@iastate.edu)

SIDA 22(1): 79 - 95. 2006

hundred years (McClure 1973; Li 1997; Judziewicz et al. 1999), with older treatments including upwards of 400 heterogeneous species from Asia, Africa, and the Americas. Currently Arundinaria is treated in a restricted sense to include only those species endemic to the eastern United States (Ohrnberger 1999), but debate continues regarding the inclusion of certain Asiatic taxa (e.g., Pleioblastus Nakai, Pseudosasa Makino ex Nakai, Bashania P.C. Keng & Yi, and Oligostachyum Z.P. Wang & G.H. Ye) that share key morphological features with the North American species (Li 1997; Judziewicz et al. 1999). However, because Arundinaria gigantea (Walter) Muhl. is the type species for the genus, its generic placement is secure. As such, Arundinaria represents the only bamboos native to North America and the only temperate bamboos (the North Temperate clade of Clark et al., in press; Zhang & Clark 2000; Kelchner & Clark 1997) native to the New World, and provides another example of the classic disjunction pattern in the flora of eastern Asia and eastern North America (Wen 1999). With a species richness ratio of approximately 20:1 up to 90:1, depending on which Asian group is used for comparison within the North Temperate bamboo clade, Arundinaria and allies also provide an example of the intriguing asymmetry within this disjunction discussed by Guo and Ricklefs (2000). Arundinaria s.s. encompasses arborescent or subarborescent woody bamboos with leptomorphic (running) rhizomes, persistent to deciduous and mostly

glabrous culm leaves, and leaves at the tip of new shoots crowded into a dis-

tinctive fan-shaped cluster or top knot with blades expanded as on foliage leaves. Branch complements typically have 1 primary branch and 0-2 subequal secondary branches arising from shortened internodes at the base of the primary branch, which rebranch to produce up to 40 or more secondary branches on older culms. The culm and foliage leaves bear fimbriae and usually also auricles. Synflorescences in this group are determinate, open, and racemose or paniculate, with 6-12 laterally compressed florets per spikelet. Spikelets have 1-2 glumes and 3 stamens per floret. Like most temperate bamboos, Arundinaria has a basic chromosome number of x = 12 and presents several enigmatic characteristics including delayed flowering and monocarpy; reproduction is primarily vegetative and seed production is infrequent and unpredictable. Arundinaria s.s. is confined to southeastern portions of the continental United States (specifically Alabama, Arkansas, Delaware, Florida, Illinois, Indiana, Kentucky, Louisiana, Maryland, Mississippi, Missouri, New Jersey, North Carolina, Ohio, Oklahoma, South Carolina, Tennessee, Texas, Virginia, and West Virginia), occurring from the Coastal Plain from New Jersey south to Florida and west to eastern Texas, and inland through the Piedmont to moderate elevations in the Appalachian Mountains. Arundinaria once formed extensive and dense canebrakes (with or without tree canopy) covering vast areas of fertile river bottomland often described by early explorers in the pre-colonial U.S. (West 1935), but has been greatly reduced in extent and abundance from

its historical range by grazing and fire suppression (Hughes 1951, 1957, 1966; Platt & Brantley 1997; Judziewicz et al. 1999).

81

Two species (Arundo gigantea Walter, Arundo tecta Walter) were originally described by Walter (1788) and represent extremes of morphological types found among inland and coastal forms, sometimes referred to as "Mississippitype" and "Atlantic-type" (sensu Gilly 1943). Arundinaria gigantea (Walt.) Muhl. (river cane or giant cane) forms extensive colonies in low woods, moist ground, and along riverbanks from the lowlands east of the Appalachians, west to Missouri, up the Mississippi Valley to southern Illinois and up the Ohio River to southern Ohio. Arundinaria tecta (Walt.) Muhl. (switch cane) forms colonies in non-alluvial swamps, moist pine barrens, live oak woods and along sandy margins of streams, preferring moister sites than A. gigantea. It is restricted to the Coastal Plain of the southeastern U.S., from southern Maryland to Alabama and Mississippi (McClure 1973; Hitchcock 1951). Within Arundinaria s.s., complex population-level variation has continued to be problematic for taxonomists and field botanists (McClure 1973; Judziewiczet al. 1999; Platt & Brantley 1997). Phenotypic diversity among North American cane populations has inspired diverse taxonomic interpretations, generally with 1-3 taxa recognized at either specific or subspecific levels (Gilly 1943; Young & Haun 1961; Voight & Mohlenbrock 1964; Radford et al. 1968; Hitchcock 1971; McClure 1973; Campbell 1985; Tucker 1988; Platt & Brantley 1997). McClure (1973) published the most recent exhaustive treatment of Arundinaria and took a conservative approach, recognizing a single polymorphic species (A. gigantea) and three subspecies, one of which [A. gigantea ssp. macrosperma (Michx.) McClure] is a catch-all for putative hybrids derived from the introgression of the other two. However, McClure acknowledged that further studies, particularly genetic-based studies, were necessary to clarify the phylogeny and taxonomy of this group. In the Southern Appalachians, astute botanical observers have long questioned the identity of a curious short-statured cane that typically occupied sites away from streams and rivers. Among the diverse North American populations of Arundinaria, a variety with deciduous foliage was recorded by botanist C.D. Beadle in Western North Carolina (Beadle 1914; see also Young 1945). Beadle recognized this form as A. tecta var. decidua, not ruling out the possibility that it might in fact be a distinct species. It is unclear why Beadle associated this deciduous variety with A. tecta, although perhaps it was because of the small stature typically associated with A. tecta. In the first half of the nineteenth century, two botanists affiliated with the University of North Carolina Herbarium, William Willard Ashe and William Chambers Coker, made notes on specimens collected near Highlands, North Carolina indicating that the short, delicate, deciduous cane of the mountains might be a distinct taxon. Roland Harper (1928) was also intrigued by cane specimens occurring on bluffs in northern

Alabama and thought that an unrecognized taxon might be present. In the latter half of the twentieth century, botanists and ecologists have informally considered the small, upland cane as "hill cane" and have been unconvinced that it could be assigned to either A. gigantea or A. tecta. Hill cane is often common in mesic and submesic slopes and upland woodlands. Moreover, because of overlapping morphological characteristics, floristic descriptions of A. tecta and A. gigantea may be confounded by this distinct form of cane. For example, Arundinaria tecta has been described as occurring along river branches 450 to 580 feet above sea-level on the southeast slopes and along the courses of mountain streams and shady mesic hillsides in the foothill region, well back from water (Harper 1928; Peattie 1929), but these inland and upland habitats almost certainly are populated by hill cane, not switch cane. In our field work on Arundinaria, we located several widespread populations of hill cane along the southern Appalachian Mountain chain, extending the range of the form that Beadle described. Field work has been complemented by herbarium studies to produce our current understanding of the range for this entity. Species limits within Arundinaria s.s. have not been examined previously in a phylogenetic framework or with molecular tools. Our investigation of hill cane is part of a larger study of the phylogenetic history of the North Temperate bamboo clade (in collaboration with the Bamboo Phylogeny Group), and as part of that study we are reconstructing the phylogeny of river cane, switch cane, and hill cane utilizing Amplified Fragment Length Polymorphism (AFLP) data to test the monophyly of putative species and to correlate the results with morphological and geographical characters, with the goal of producing a revised treatment of the genus. Ordination analyses (PCA) of morphological characters and AFLP studies will be presented in a later publication. Preliminary cladistic analysis of AFLP data (Triplett & Clark, in prep.) demonstrated that the three types of cane form separate monophyletic lineages encompassing two previously recognized entities (river cane and switch cane) and one entity encompassing those plants recognized as hill cane. Moreover, hill cane specimens from a wide geographic range cluster as the sister clade of A. tecta, rejecting the hypothesis that hill cane is an ecologically induced form of A. tecta and instead suggesting that it is a distinct lineage with a unique evolutionary history. These results prompted a reevaluation of diagnostic characters within Arundinaria s.s. Preliminary ordination (PCA) analyses of morphological characters similarly identified three non-overlapping entities and allowed us to recognize the most important diagnostic vegetative features. These groups correspond precisely with the three lineages derived from the AFLP data. We therefore propose the recognition of each entity at the species level: A. gigantea (river cane), A. tecta (switch cane) and a previously undescribed species (hill cane). In advance of the publication of the Flora of North America, we here describe and illustrate the new species, A. appalachiana Triplett, Weakley, &

L.G. Clark, from the southern Appalachian Mountains, and compare and contrast it with its congeners A. gigantea and A. tecta.

MATERIALS AND METHODS

Field studies of natural populations were conducted in October 2003 and July-October 2005. Standard bamboo collection procedures were followed (Soderstrom & Young 1983); bulky specimens of rhizomes, branch complements, and culm nodes and internodes were made for all collections. Herbarium specimens from A, F, GA, GH, ISC, NCU, and US (herbarium acronyms following Holmgren & Holmgren 2006) were examined. While our taxonomic circumscription of Arundinaria s.s. is based on an approach combining morphological and molecular data, we have relied upon morphological characters to provide identifications of the specimens examined. Complete specimens, including culm leaves, buds, branch complements with foliage leaves, and synflorescences were rarely available, and some herbarium specimens of Arundinaria could not be conclusively assigned to species. Only one flowering specimen was located among the specimens identified as A. appalachiana. Specimens were measured for a variety of morphological characters, including foliage leaf length and width, inner ligule length, inflorescence length, spikelet length, and lengths of spikelet bracts (glumes I-IV, lemma and palea). Top knot (the cluster of leaves at the tip of new shoots) and foliage leaf lengths were measured from the base of the pseudopetiole to the tip of the blade. Leaf width was measured at the widest point. Primary branch length was measured from the point of origin at the node to the end of the branch axis. Synflorescence length was measured from the base of the basalmost branch to the apex of the main axis. Spikelets were removed from specimens and softened using a modified Pohl's solution (Pohl 1965; 750 ml distilled water, 250 ml 1-propanol, 2 ml liquid dish soap), dissected, examined, and measured for floral characters using a dissecting microscope equipped with a micrometer. Anatomical characters of leaf blades (both epidermal micromorphology and cross sections) were obtained using light microscopy of sections made following standard protocols for free hand sectioning and epidermal peels (Clark 1986; Ellis 1976, 1979).

RESULTS AND DISCUSSION

Our decision to recognize this taxon at the species level is based upon the combination of phylogenetic and morphologic analyses with careful consideration of the decisions made in the past regarding the North American Arundinaria species complex and the ability to diagnose monophyletic units. This interpretation follows from morphological (i.e., diagnostic characters) and phylogenetic (i.e., unique ancestry) species concepts (Olmstead 1995; Sites & Marshall 2003). The features discussed below are those identified as the most diagnostic based

on observations made during field work and morphological ordination analyses (PCA). The most consistent differences among the North American species are seen in vegetative characters including features of the rhizomes, culm internodes and culm leaves, branching, and top knot and foliage blades, described below and summarized in Table 1.

Distribution & ecology

Arundinaria appalachiana is indigenous to the southern Appalachian Moun-

tains where it occurs in the southern Blue Ridge, Blue Ridge/Piedmont Escarpment, upper Piedmont, and Ridge and Valley physiographic provinces (Fig. 1). The full extent of its distribution is still poorly known, because of the infrequent collection of bamboos in eastern North America and the often poor quality of the existing specimens; for this reason we have chosen to supplement vouchered specimens with additional county records based on what we consider reliable sight records of this new species (these counties should be verified with vouchers). Hill cane is common in oak-hickory forests and woodlands on mesic, submesic, and xeric slopes and uplands, sometimes occurring as well in hillside seepages, but nearly always on slopes, bluffs, and ridges away from perennial streams, in contrast to the geographically sympatric A. gigantea. Associated overstory species include Quercus montana Willd., Q. coccinea Münchh., Q. alba L., Q. rubra L., Q. falcata Michx., Pinus echinata Mill., P. virginiana Mill., Carya alba (L.) K. Koch, Carya glabra (Mill.) Sweet, and Nyssa sylvatica Marshall. Although these slope and ridge forests are well-drained, the annual rainfall amounts in this region are high and equably distributed. In the escarpment gorges of the Chattooga River, Whitewater River, Thompson River, Horsepasture River, Toxaway River, Horsepasture River, and Eastatoe Creek, the highest annual rainfalls in eastern North America (exceeding 80 inches a year) maintain higher then expected moisture levels even in topographic situations that tend to create xeric communities (ridgetops and convex upper slopes and side ridges) (Robinson 2000). Still, there is no question that hill cane occupies unusually dry and upland habitats compared to its congeners. Arundinaria gigantea typically occurs on the floodplains of large to small rivers, sometimes edging onto lower portions of mesic slopes, whereas A. tecta typically occurs along small to medium blackwater rivers, in swamps, on deep peat in pocosins, and in small seepages with organic soils. Arundinaria appalachiana is sympatric (at least in the broadest sense) with both of its congeners, in that it occurs in the same counties and within a few kilometers of populations of both A. gigantea and A. tecta. Within the region occupied by A. appalachiana however, A. gigantea occurs only along the upper reaches of major rivers, notably the Little Tennessee and French Broad Rivers, while A. tecta also occurs at lower elevations and in different topographic and ecological situations.

TABLE 1. Morphological comparisons of Arundinaria appalachiana, A. tecta, and A. gigantea.

Character	A. appalachiana	A. tecta	A. gigantea
Rhizome air canals Sulcus Culm leaf duration	present or absent usually absent persistent	present usually absent persistent	absent usually present deciduous
Culm leaf auricles	absent	, present, deciduous	present, deciduous

Top knot number of leaves	6-12	9–12	6-8
Top knot leaf blade length (cm)	9-22.5	20-30	16-24
Compressed basal internodes on primary branch	2–5	2-4	0-1
1° branch basal nodes: 2° branches	absent	present, subequal	present, subequal
Primary branch length (cm)	7–33	usually >50	15-25
Foliage leaf blade length (cm)	5-20	7–23	8-15
Foliage leaf blade width (cm)	0.8-2	1-2	0.8-1.3
Foliage leaf vestiture	pilose or glabrous	densely pubescent or glabrous	densely pubescent or glabrous
Foliage leaf duration	deciduous	evergreen	evergreen
Foliage leaf texture Foliage leaf abaxial tessellation	chartaceous weakly tessellate	coriaceous strongly tessellate	subcoriaceous strongly tessellate

The species biology of *A. appalachiana* is poorly understood. Its congeners are long-lived monocarpic perennials, and this appears to be the case with *A. appalachiana* as well. It has been seen flowering and fruiting even more infrequently than its congeners; judging from its habitat, its flowering and fruiting may be stimulated by fire (like *A. tecta*), and the paucity of fertile specimens may reflect the general suppression of fire in its habitat through the twentieth century. Field observations suggest that clones of *A. appalachiana* are slow-growing and very long-lived, certainly persisting for decades and likely for centuries.

Morphology

Rhizomes.—The rhizomes of *A. appalachiana* are leptomorphic, a characteristic they share with other north temperate woody bamboos; however, in many cases the growing tips of new rhizomes travel only a short distance before turning up to form a new culm, thus presenting a sympodial branching pattern. This pattern also occurs in *A. tecta* but has not been confirmed for *A. gigantea*. An interesting characteristic of this species is the variability in air canal development (McClure 1963). Air canals are present in some specimens but not others, and may in fact be longitudinally and peripherally discontinuous in rhizomes of *A. appalachiana*. Air canals are consistently present in *A. tecta* and are apparently continuous.

Culm internodes.—Although the culm internodes of A. appalachiana can

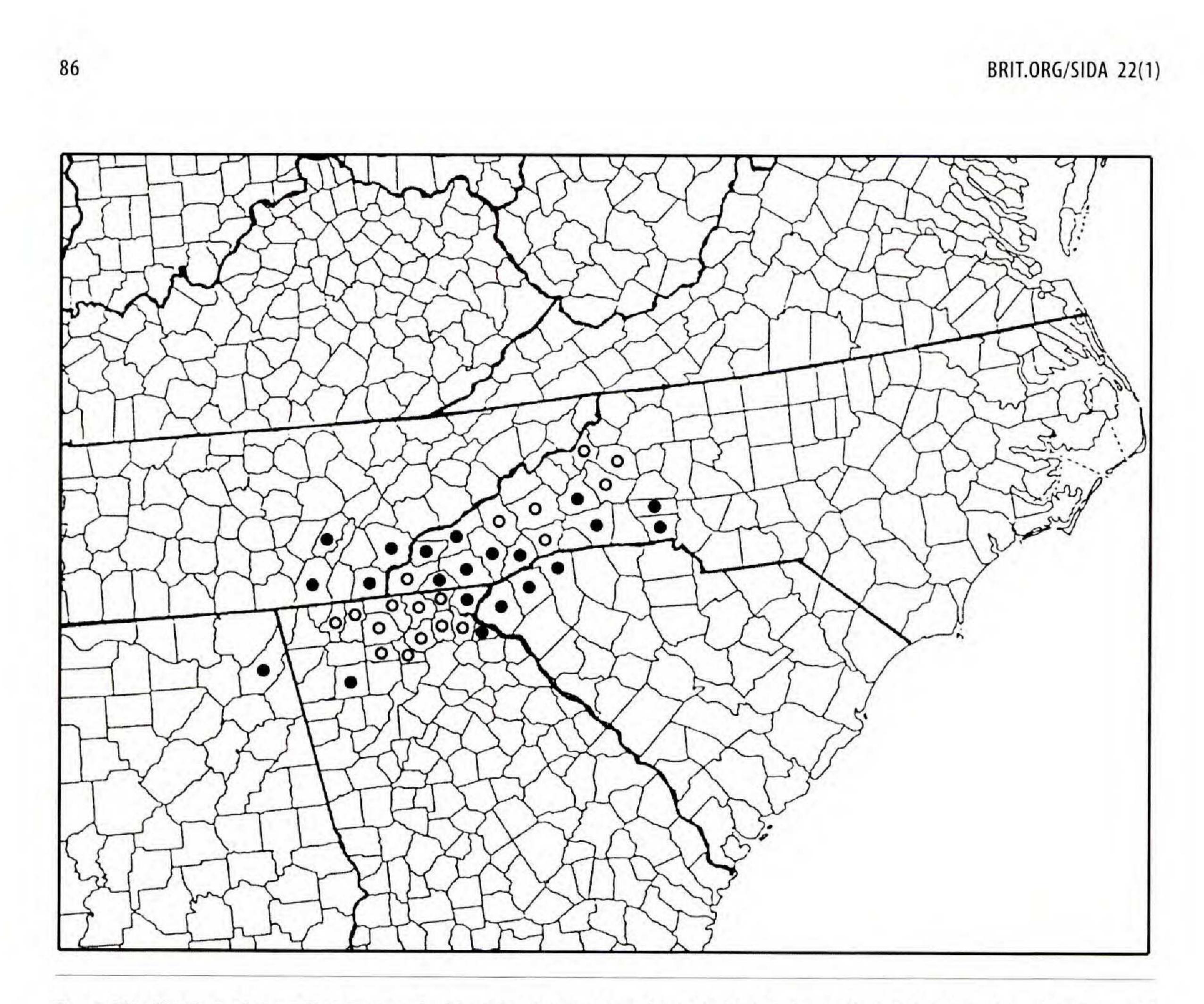


Fig. 1. Distribution of Arundinaria appalachiana in the southeastern United States. Filled circles based on documented specimens; open circles based on unvouchered sight records.

be somewhat flattened behind the branch complement, the internodes lack a prominent groove or sulcus. This is consistent with *A. tecta* but contrasts with *A. gigantea*, which typically has internodes that are prominently sulcate.

Branching.—In bamboos, the morphology and architecture of the set of branches arising from culm nodes (the branch complement) is a source of numerous taxonomically useful characters. In *Arundinaria*, the pattern of shortened or compressed internodes at the base of primary branches and the extent and pattern of secondary branching are especially valuable. The branch complement of *A. appalachiana* is characterized by 2–5 shortened or compressed internodes at the base of the primary branch, without rebranching in this basal area. The first elongated internode above the shortened ones is typically constrained to ~30% the length of distal internodes. In contrast, *A. tecta*, while having a similar pattern of compressed internodes, typically will produce buds and branches from the nodes in the area of compression, creating subequal branches from the base of the primary branch. *Arundinaria gigantea* typically has only one (or no) compressed basal internode, but if present, this node may produce a secondary branch. Primary branches in *A. appalachiana* are usually

less than 35 cm long. In contrast, *A. tecta* produces long primary branches usually >50 cm.

Culm leaves. - The culm leaves of A. appalachiana are typically shorter than their associated internodes at the base of the plant, becoming progressively longer towards the top knot. At midculm they are approximately the same length as the associated internode. In contrast, midculm culm leaves of A. tecta are longer than their associated internodes, and those of A. gigantea shorter. Arundinaria appalachiana and A. tecta have persistent culm leaf sheaths, whereas A. gigantea has deciduous sheaths. The culm leaf sheaths of A. appalachiana are tessellate; however, their tessellation is not as pronounced as it is in A. tecta. The culm leaves lack well-developed, prominent auricles, unlike A. gigantea and A. tecta. Top knot and foliage leaves. -- In Arundinaria, leaves at the tip of new culms are crowded into a distinctive fan-shaped cluster or top knot, with their blades expanded as on foliage leaves. The top knot leaf blades of A. appalachiana are typically 9-22.5 cm in length, while A. tecta typically has larger blades (20-30 cm long); those of A. gigantea are typically 16-24 cm in length. The foliage leaf blades of A. appalachiana are deciduous; bladeless branches persist on the plants after leaf drop, often with the older sheaths still intact. The blades are chartaceous; presumably, since the blades are deciduous, the plant invests less energy in producing them by producing less sclerenchyma. In contrast, the leaves of A. gigantea are persistent and subcoriaceous, while leaves of A. tecta are persistent and coriaceous. The abaxial surfaces of the leaf blades of A. appalachiana are weakly tessellate, whereas in A. gigantea and A. tecta they are strongly tessellate. The abaxial and adaxial leaf surfaces are typically sparsely to more or less densely pilose (glabrous in some populations) in A. appalachiana. Leaf blades of A. gigantea are typically densely pubescent with short, soft hairs on abaxial surfaces, while the blades of A. tecta are densely pubescent on both surfaces; neither of these pubescence patterns has been seen in A. appalachiana. It is important to note that Arundinaria gigantea and Arundinaria tecta can both survive in deeper shade in the forest, albeit in stunted conditions, and thus it is possible to find diminutive or depauperate plants of both that superficially resemble hill cane, mostly in stature. However, a combination of characters such as the branch complement, leaf texture, and leaf pubescence are usually sufficient to distinguish these stunted forms of river and switch cane from hill cane populations and from each other.

TAXONOMIC TREATMENT KEY TO THE SPECIES OF ARUNDINARIA SENSU STRICTO

 Primary branches with 0–1 compressed basal internodes; culm internodes usually sulcate; culm leaves deciduous _____ A

A. gigantea

87

A.tecta

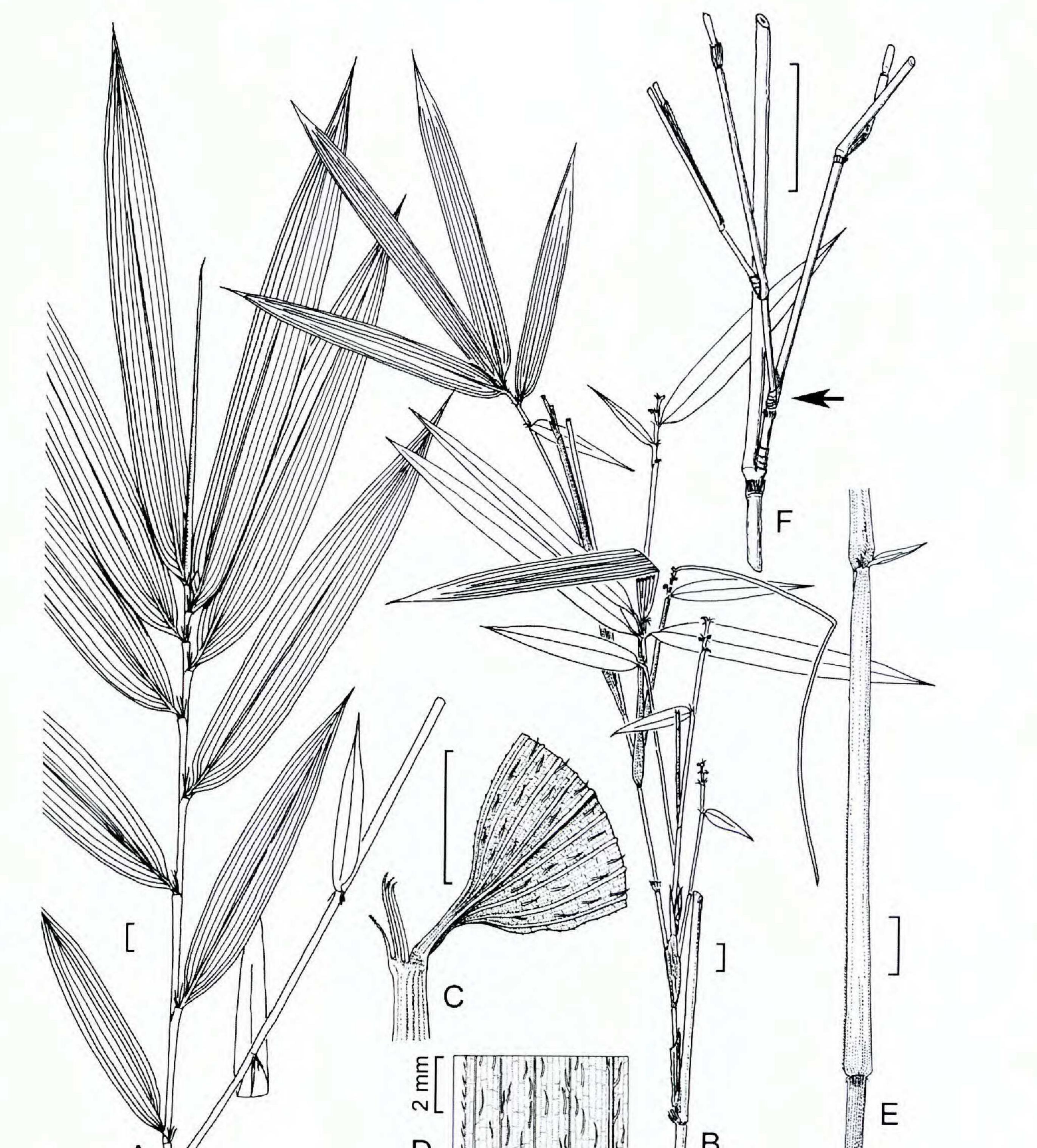
 Primary branches with 2–5 compressed basal internodes; culm internodes usually terete; culm leaves persistent to tardily deciduous.

88

- 2. Foliage blades coriaceous, persistent, abaxial surfaces densely pubescent or glabrous, strongly tessellate; primary branches usually more than 50 cm long, basal nodes developing secondary branches; top knot blades 20–30 cm long _____
- 2. Foliage blades chartaceous, deciduous, abaxial surfaces pilose or glabrous, weakly tessellate; primary branches usually less than 35 cm long, basal nodes not developing secondary branches; top knot blades 9–22.5 cm long _____ **A. appalachiana**

Arundinaria appalachiana Triplett, Weakley & L.G. Clark, sp. nov. (Figs. 1–5). Түре: UNITED STATES. Alabama: Dekalb Co.: Desoto State Park by Rt. 89 (34° 30' N Lat.; 85° 38' W Long.), elev. ca. 515 m, 25 Jul 2005, *Triplett & Ozaki* 99 (Holotype: ISC; Isotypes: MO, NCU, UNA, US).

Rhizomata leptomorpha, strato cavernularum aëriarum interdum praesenti. Culmi 2-6 mm diametro, 0.5-1.8 m alti, omnino glabri, erecti. Internodia 4.5-12 cm longa, teretia (sine sulco). Vaginae culmorum 5.5-11(-15) cm longae, persistentes, sine auriculis. Culmi juniores fasciculo terminali (5-)6-12 foliorum, laminis (5-)9-22.5 cm longibus, 1.4-2.8 cm latibus, linearibus vel lineari-lanceolatis vel ovatilanceolatis, pilosis vel interdum glabris. Rami primarii ad nodos medianos culmorum 1, 7-33 cm longi, internodiis abbreviatis sine gemmis basi 2-5. Folia cujusquisque complementi 3-7. Laminae foliorum (3-)5-20 cm longae, 0.5-2 cm latae, chartaceae, deciduae, pilosae vel interdum glabrae, abaxialiter infirme tessellatae. Synflorescentiae 7-11.5 cm longae, 2-5 cm latae, determinatae racemosae apertae; pedicelli 4-25 mm longi, spiculis 6-8. Spiculae 3-5.5 cm longae, glumis 1(-2), flosculis basilibus interdum sterilibus, 5-8 flosculis fertilibus continentibus et anthoeciis rudimentalibus terminalibus 1-3; glumae inaequales, 5-nervatae, attenuatae, glabrae; gluma I 3-6.5 mm longa; gluma II 5.5–9 mm longa; lemmata fertilia 11–16 mm longae, 7–11-nervata, apicibus acutis vel acuminatis, abaxialiter glabris; palea 10–13 mm longa, 8–10-nervata. Stamina 3; anthera 5–7 mm longa. Woody bamboo. Plants of diffuse to (pluri-) caespitose habit. Rhizomes leptomorphic, usually horizontal for a only short distance before turning up at the apex to form a culm (therefore often presenting a sympodial branching pattern), hollow (with a small central lumen), peripheral air canals sometimes present (if so, apparently discontinuous longitudinally and/or peripherally). Culms 2-6 mm in diameter, 0.4-1.8 m tall, erect, tillering; internodes 4.5-12 cm long (progressively shorter towards culm apex), terete, hollow, glabrous, flattened behind the branch complement on larger culms but the sulcus not prominent; nodes solitary, the nodal line horizontal, supranodal ridge not prominent; bud one per node (single) on a slight promontory, triangular, the shoulders of the prophyll ciliate. Culm leaves persistent, approximately equaling associated internodes at midculm, typically shorter than associated internodes at the culm base, becoming proportionally longer towards the culm apex; sheaths 5.5-11 (-15) cm long, shortest on lower nodes, becoming progressively longer towards the culm apex, glabrous, margins ciliate; blades 0.5-1.4 cm long, triangular to lanceolate, reflexed to erect, glabrous, deciduous, intergrading into top knot leaves; auricles absent; fimbriae 1-9 mm long, ascending to erect; inner ligules ca. 0.1 mm long, a fringe of short cilia; outer ligule absent. Top knot leaves in an apical cluster of (5-)6-12; sheaths glabrous, margins ciliate; auricles absent; fim-



89

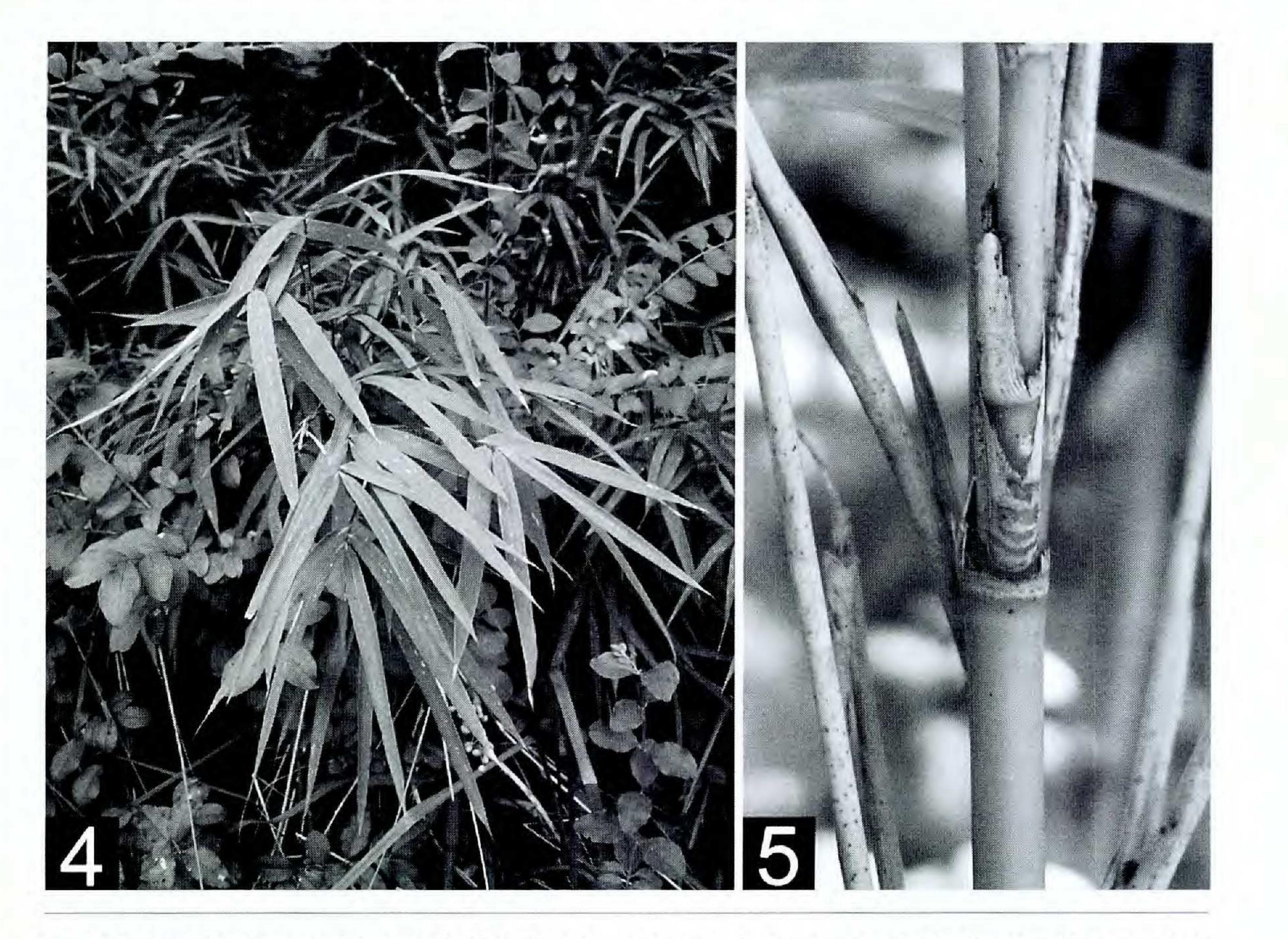
Fig. 2. Arundinaria appalachiana. A. Top knot of new shoot. B. Foliage leaf complement from midculm node. C. Foliage leaf, showing apex of sheath, fimbriae, pseudopetiole, and base of blade. D. Detail of abaxial surface of blade showing tessellation and pilose vestiture. E. Culm leaf at midculm node. F. Branch complement showing compressed basal internodes and reiterative secondary branch (arrow). Scale bar = 1 cm unless otherwise noted. All drawings based on *Triplett & Ozaki 99*. (Illustrations by J. Triplett)



Fig. 3. Arundinaria appalachiana. A. Partially dissected spikelet showing two florets. B. Synflorescence with five spikelets. Scale bar = 1 cm. Drawings based on Ahles & Leisner 15147. (Illustrations by J. Triplett)

briae 1–9 mm, ascending to erect; **blades** (5–)9–22.5 cm long, 1.4–2.8 cm wide, L:W = 8.3–9.3, linear, linear-lanceolate or ovate-lanceolate, chartaceous, pilose or glabrous, abaxially weakly tessellate, apices acuminate, bases attenuate to cuneate, midrib \pm centric. **Branching** infravaginal (rarely extravaginal); **primary branches** 1 per node, 7–33 cm long, with 2–5 compressed basal internodes, basal nodes not developing secondary branches; first elongated internode shorter than subsequent ones (~30%); **higher order branches** present on older plants, reiterating the 1° branch (i.e., with the same pattern of compressed basal internodes and branching). **Foliage leaves** 3–7 per complement; **sheaths** glabrous, margins ciliate, weakly tessellate; **auricles** absent; **fimbriae** 1–9 mm, ascending to erect;

inner ligule glabrous or ciliate, fimbriate or lacerate; **outer ligule** present as a minute rim; **blades** linear, linear-lanceolate, or ovate-lanceolate, chartaceous, deciduous, surfaces pilose (sometimes glabrous), abaxially weakly tessellate, apices acuminate, bases attenuate to cuneate, midrib ± centric; primary branch foliage leaf blades (4–)9–20 cm long, (0.5–)0.8–2 cm wide; L:W = 10.7–11.7; higher order branch foliage leaf blades (3–)5–17.5 cm long, (0.5–)0.8–1.5 cm wide; terminal foliage leaf blade rarely unexpanded laterally, withering but persisting as a tail-like appendage. **Synflorescences** 7–11.5 cm long, 2–5 cm wide, determinal



91

FIGS. 4-5. Arundinaria appalachiana. 4. Habit, in Rhea Co., Tennessee. 5. Close-up of primary branch with compressed basal internodes, Dekalb Co., Alabama. (Photos by J. Triplett)

nate, open-racemose, apparently borne on specialized nonleafy shoots; peduncle 10-17 cm long (3 measured), glabrous, terete; rachis glabrous; pedicels 4-25 mm long; 6-8 spikelets per synflorescence. Spikelets 3-5.5 cm long, laterally compressed, disarticulating above the glumes and between the florets, consisting of 1(-2) glumes, occasionally a basal sterile floret, 5-8 fertile florets and 1-3 progressively rudimentary apical sterile florets; rachilla internodes 3-4 mm long; glumes unequal, 5-nerved, attenuate, glabrous; glume I 3-6.5 mm long; glume II 5.5-9 mm long; fertile lemmas 11-16 mm long, 7-11-nerved, apex acute or acuminate, abaxially glabrous, transverse veinlets barely perceptible or not at all manifest, usually somewhat reddish-purple; paleas 10-13 mm long, 8-10nerved, broadly sulcate and 2-keeled dorsally; lodicules and ovary not seen. Sta-

mens 3; anthers 5-7 mm long. Fruit not seen.

Distribution and Ecology.—(Fig. 1). Endemic to the southern Appalachians and upper Piedmont of northeastern Alabama, northern Georgia, southwestern North Carolina, northwestern South Carolina, and southeastern Tennessee, United States; 300-800(-1065) m. In upland oak-hickory-pine forests on slopes, less typically in more mesic sites, seeps, or along small streams. Phenology.-Lack of specimens in flower or information on the extent of

blooming makes it impossible to determine flowering behavior in this species at present. Of the specimens cited below, only one confirmed flowering specimen of this species was identified, suggesting that flowering may be an even rarer event in this species than in most woody bamboos.

Etymology.—*Arundinaria appalachiana* is named for its distribution in the forests of the Appalachian Mountains.

Common name.—hill cane.

Representative specimens examined: UNITED STATES. ALABAMA. Dekalb Co.: Little River Canyon National Preserve, plot PIEC 27, 2002, McDaniel s.n. (NCU); in steep wooded bank of West Fork, Little River, across stream from overlook shelter, DeSoto State Park, 9 May 1959, Sherman & Carter 25747 (GH); Desoto State Park on trail by Laurel Creek (34° 30' N Lat; 85° 38' W Long.), elev. ca. 515 m, 25 Jul 2005, Triplett & Ozaki 100 (ISC, MO, US). GEORGIA. Bartow Co.: in woods on S side of Stamp Creek Rd. just E of Jones Mill Rd. (34° 14' N Lat; 84° 40' W Long.), elev. ca. 311 m, 26 Sep 2005, Triplett 166 (ISC, MO, US). Rabun Co.: maple-birch-magnolia association, Laurel Creek Olivine Deposit, 1.5 mi E of Pine Mt., 21 Jun 1946, Radford s.n. (NCU); oak-hickory woods on Pine Mt., Bald Rd., 4 Jun 1952, Radford 6134 (NCU); Warwoman Road and Overflow Creek bridge, N side, 20 May 1996, Stancil 950 (GA); in swamp near top of Oakey Mountain, SE of Nacoochee Reservoir, 25 May 1941, Duncan 3283 (GA); on trail from 155 0.5 mi S of Kattie Place, elev. ca. 790 m, 22 Oct 1995, Milsted & Zhang 585 (GA); pine-oak woodland near roadside park, 1 mi N of Tallulah Falls River, 9 May 1967, Isely, Welsh, & Isely 10286 (ISC); 2 mi N of Warwoman Rd. along GA 28, scattered throughout mature woods W of road (34° 57' N Lat; 83° 10' W Long.), elev. ca. 687 m, 25 Oct 2003, Triplett & Clark 20 (ISC, MO, US). Stephens Co.: Deep gorge, Cedar Creek, Camp Mikell Rd. off GA 184, just W of Camp Mikell and N of Toccoa (34 08' 06" N. lat.; 83 20' 13" W. long), elev. ca. 300 m, 19 Jun 1975, Boufford & Wood 16501 (NCU); NWfacing ravines and ridges on the S side of Panther Creek, SW of Yonah Lake (Tugaloo River), N of Toccoa (34 43' 30" N. lat.; 83 21' 13" W. long.), 25 Jun 1975, Boufford & Wood 16766 (NCU). NORTH CAROLINA. Clay Co.: Oak-hickory woods, 4 mi NW of Hayesville, 5 Jun 1952, Radford & Wood 6162 (NCU). Gaston Co.: low woodland near the northern tip of Pasour Mt., about 3 mi SSW of High Shoals, 21 Jun 1956, Ahles & Leisner 15147 (NCU); oak-hickory woods on Crowder's Mt., 4 Jun 1953, Radford 7084 (NCU). Graham Co.: small population on N side of Santeetlah Dam Rd. (SR 1146) just off Hwy 129 (35° 22' N Lat; 83° 51' W Long.), elev. ca. 537 m, 2 Oct 2005, Triplett 185 (ISC, MO, US). Jackson Co.: on highway between Dillsboro & Park Entrance, extensive clump on the top of bank by roadside, 26 Jul 1937, Coker s.n. (NCU); Cope Creek Rd. just off NC 23 out of Sylva, growing among Polytrichum sp., Pine, and sedge (35° 23' N Lat; 83° 11' W Long.), elev. ca. 675 m, 25 Oct 2003, Triplett & Clark 21 (ISC, MO, US). Lincoln Co.: rich deciduous forest and stream banks 0.4 mi W of Cat Square, 28 Apr 1957, Bell 6638 (NCU). Macon Co.: maple-birch-magnolia (cove) association, Corundum Hill Olivine Deposit, 11/2 mi NW Gneiss, 15 Jun 1946, Radford s.n. (NCU); Horse Cove near Highlands, 3 Sep 1948, Radford s.n. (NCU); in deep, shaded ravine at top of pasture at foot of Whiterock Mountain, 7 mi from Otto, NC on Tessentee Creek Rd., elev. ca. 1065 m, 7 Aug 1938, Stewart & Hechenbleikner s.n. (NCU); pine-broom-straw association, Corundum Hill Olivine Deposit, 1.5 mi NW Gneiss, 15 Aug 1946, Radford s.n. (NCU); Mulberry Rd. ca. 0.5 mi off 441, on steep hillside among oak, rhododendron, and maple (35° 01' N Lat; 83° 23' W Long.), elev. ca. 647 m, 25 Oct 2003, Triplett, Clark, & Weakley 19 (ISC, MO, US). McDowell Co.: near Marion, 25 Oct 1915, Ashe s.n. (NCU). Polk Co.: 4 mi W of Tyron, valley of Fall Creek in wet meadow on peninsula in reservoir, 19 Jun 1942, Walker 3469 (US). Rutherford Co.: wet ditch on CR 1721 2 mi N of Sunshine, 24 Jun 1967, Smith 74 (NCU). Swain Co.: Bryson City, by stream, 11 Jul 1927, Hunnewell s.n. (GH); Bryson City, private property on W side of Wiggins Rd., 0.3 mi up from Betts Branch (SR 1343) (35° 26' N Lat; 83° 25' W Long.), elev. ca. 601 m, 1 Oct 2005, Triplett 184 (ISC, MO, US). Transylvania Co.: rocks and cliffs on side of mountain, 100 to 200 feet above the bank of Davidson River, Pisgah Forest, 28 Sep 1915, Ashe s.n. (NCU); Pisgah Forest, road to

Pink Beds, 23 Aug 1938, Stewart s.n. (NCU); Middle Bearcamp Creek area, roadside, Highlands, 2 Aug 1962, Rodgers & Shake 62165a (NCU); oak woods near Looking Glass Falls, 7 Jun 1952, Radford & Wood 6192 (NCU); Horsepasture Gorge, roadside about 1 mi W of crossing, elev. ca. 488 m, 8 Jun 1961, Rodgers 6162a (NCU). SOUTH CAROLINA. Greenville Co.: Cedar Mountain, 0.4 mi down gravel road 3.8 mi S of Caesar's Head SP Visitor Center (35° 05' N Lat; 82° 36' W Long.), elev. ca. 515 m, 30 Sep 2005, Triplett 179 (ISC, MO, US). Oconee Co.: oak-hickory woods, ridge above Walhalla Fish Hatchery, ca. 11 mi N of junction of S.C. Routes 28 and 107 on Route 107, 9 Jun 1952, Wood 7879 (A); Hill property, NW side Old Rocky Gap Road, W side West Village Creek near creek, Mountain Rest, Blue Ridge province, elev. ca. 520 m., 24 Aug 1991, Hill 22585 (GH). Pickens Co.: mixed deciduous forest, 3 mi N of Rocky Bottom near US 178, 22 Aug 1956, Radford 16758 (NCU); Boggs' Rock, granite-gneiss outcrop N of Liberty, 3 Jun 1974, Knox 407 (NCU); Rich wooded slope, 2.4 mi S of NC line on US 178, 8 Jun 1956, Ahles & Bell 14298, (NCU). TENNESSEE. Hamilton Co.: Lookout Mt. Nat. Military Park, Chattanooga, 1 small plant at summit of mountain, in hardwood forest., 29 Jun 1957, Pohl 7664A (ISC). Monroe Co.: White Cliff Springs, Jul 1890, Lamson-Scribner s.n. (US). Polk Co.: Boyd Gap Overlook above Ocoee River, 4.2 mi W of Hwy 68, on steep wooded hillside just beyond entrance to Boyd Gap Trail #331 (35° 02' N Lat; 84° 27' W Long.), elev. ca. 529 m, 26 Sep 2005, Triplett 165 (ISC, MO, US). Rhea Co.: Firetower Rd just off Hwy 68 next to Grandview Community Center and below intersection with Emergency Road (35° 44' N Lat; 84° 50' W Long.), elev. ca. 445 m, 3 Oct 2005, Triplett 188 (ISC, MO, US).

93

ACKNOWLEDGMENTS

Field work was supported by a Graduate Research Grant from the American Society of Plant Taxonomists and grants from the American Bamboo Society to JT as well as a National Geographic Society Grant (#7336-02) to LC. Support for JT and for the final preparation of this manuscript came from a National Science Foundation Grant (DEB-0515712) to LC. We are indebted to Angus Gholson (Chattahoochee, FL), Michael Hotchkiss (USDA, Byron, GA), Robert and Lauren Clark (Peachtree City, GA), Jim and Frankie Triplett (Winston-Salem, NC), Gary Kauffman, Linda Lee Leslie, Adam and Sue Turtle (Earth Advocates Research Farm, Summertown, TN), and Julian Campbell (TNC, Lexington, KY) for their hospitality or assistance in locating populations of Arundinaria. We also thank the curators of the herbaria that loaned specimens for this study. We are grateful to Gary Kauffman, Keith Langdon, Virginia McDowell, Tom Govus, and Mike Schafale for their interest and assistance in resolving the persistent taxonomic issue of the correct identity of the small upland mountain cane. Chris Stapleton (Royal Botanic Gardens, Kew) kindly pointed out to us the importance of compressed internodes in the taxonomy of

this group and Emmet Judziewicz (Dept. of Biology, University of Wisconsin-Stevens Point) suggested the specific epithet.

REFERENCES

BEADLE, C.D. 1914. Bamboo. In: Bailey, L.H. The standard cyclopedia of horticulture, Vol. 1.
 New York: The Macmillan Company. P. 446.
 CAMPBELL, J.N. 1985. The land of cane and clover: presettlement vegetation in the so-called

bluegrass region of Kentucky. Herbarium Report, University of Kentucky, Lexington.

CLARK, L.G. 1986. Systematics of *Chusquea* Section *Chusquea*, Section *Swallenochloa*, Section *Verticillatae*, Section *Serpentes*, and Section *Longifoliae* (Poaceae: Bambusoideae). Unpublished Ph.D. dissertation, Iowa State University, Ames.

CLARK, L.G., S. DRANSFIELD, J. TRIPLETT, and J.G. SÁNCHEZ-KEN. (In press). Phylogenetic relationships among the one-flowered, determinate genera of Bambuseae (Poaceae: Bambusoideae). In: Columbus, J.T., E.A. Friar, C.W. Hamilton, J.M. Porter, L.M. Prince, and M.G. Simpson, eds. Monocots: comparative biology and evolution. 2 vols. Rancho Santa Ana Botanic Gar-

den, Claremont, California, U.S.A.

94

ELLIS, R.P. 1976. A procedure for standardizing comparative leaf blade anatomy in the Poaceae. I. The leaf blade as viewed in transverse section. Bothalia 12:65–109.
ELLIS, R.P. 1979. A procedure for standardizing comparative leaf blade anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia 12:641–672.
GILLY, C.L. 1943. A preliminary investigation of the North American canes (Arundinaria). Bull. Torrey Bot. Club, 70:297–309.

Guo, Q. and R.E. RICKLEFS. 2000. Species richness in plant genera disjunct between temperate eastern Asia and North America. Bot. J. Linn. Soc. 134:401–423.

HARPER, R.M. 1928. Economic botany of Alabama. Part 2. Catalogue of the trees, shrubs, and vines of Alabama, with their economic properties and local distribution. Geol. Survey Alabama Monogr. 9:1–357.

Нітснсоск, А.S. 1951. Manual of grasses of the United States. Rev. by Agnes Chase. 2nd ed. USDA Misc. Pub. 200, U.S. Government Printing Office, Washington, DC.
Нітснсоск, А.S. 1971. Manual of the grasses of the United States. Dover Publ., New York.
Ноімдяєм, Р.К. and N.H. Ноімдяєм. 1998 onwards (continuously updated). Index herbariorum. New York Botanical Garden. http://sciweb.nybg.org/science2/IndexHerbariorum.asp
Ниднєя, R.H. 1951. Observations of cane (*Arundinaria*) flowers, seed, and seedlings in the North Carolina coastal plain. Bull. Torrey Bot. Club 78:113–121.

- HUGHES, R.H. 1957. Response of cane to burning in the North Carolina coastal plain. North Carolina Agric. Exp. Stat. Bull. 402.
- HUGHES, R.H. 1966. Fire ecology of canebrakes. Proceedings of the Fifth Annual Tall Timbers Fire Ecology Conference, March 24–25, 1966. Mimeographed.
- JUDZIEWICZ, E.J., L.G. CLARK, X. LONDONO, and M.J. STERN. 1999. American bamboos. Smithsonian Institute Press, Washington, DC.

KELCHNER, S.A. and L.G. CLARK. 1997. Molecular evolution and phylogenetic utility of the chloroplast *rpl*16 intron in *Chusquea* and the Bambusoideae (Poaceae). Molec. Phylogen.

Evol. 8:385-397.

- Li, D.Z. 1997. The flora of China Bambusoideae Project: Problems and current understanding of bamboo taxonomy in China. In: Chapman, G.P., ed. The bamboos. Linnean Society of London Symposium Series. Academic Press, London.
- McClure, F.A. 1963. A new feature in bamboo rhizome anatomy. Rhodora 65:134–136.
 McClure, F.A. 1973. Genera of bamboos native to the New World (Gramineae: Bambusoideae). Smithsonian Contr. Bot. 9. Smithsonian Institution, Washington, D.C.
 OLMSTEAD, R.G. 1995. Species concepts and plesiomorphic species. Syst. Bot. 20:623–630.

OHRNBERGER, D. 1999. The bamboos of the World. Elsevier. Peattie, D.C. 1929. Flora of the Tyron region. J. Elisha Mitchell Sci. Soc 44:141–229. PLATT, S.G. and C.G. BRANTLEY. 1997. Canebreaks: An ecological and historical perspective. Castanea 62:8–21.

95

Ронь, R.W. 1965. Dissecting equipment and materials for the study of minute plant structures.Rhodora 67:95–96.

RADFORD, A.E., H.E. AHLES, and C.R. BELL. 1968. Manual of the vascular flora of the Carolinas.

University of North Carolina Press, Chapel Hill.

- ROBINSON, P.J. 2000. Weather and climate. In: Orr, D.M., Jr. and A.W. Stuart. The North Carolina atlas: portrait for a new century. University of North Carolina Press, Chapel Hill. Pp. 21–30.
- SITES, J.W. JR. and J.C. MARSHALL. 2003. Delimiting species: a renaissance issue in systematic botany. Trends Ecol. Evol. 18:462–470.
- Soderstrom, T.R. and S.M. Young. 1983. A guide to collecting bamboos. Ann. Missouri Bot. Gard. 70:128–136.
- TUCKER, G.C. 1988. The genera of Bambusoideae (Gramineae) in the southeastern United States. J. Arnold Arbor. 69:239–273.
- Voight, J.W. and R.H. Mohlenbrock. 1964. Plant communities in southern Illinois. Southern Illinois University Press, Carbondale.
- WALTER, T. 1788. Flora Caroliniana. J. Fraser, London.
- WEN, J. 1999. Evolution of eastern Asian and eastern North American disjunct distribu-

tions in flowering plants. Ann. Rev. Ecol. Syst. 30:421–455.

- WEST, E.M. 1935. Canebrakes of the southeastern United States. The Ohio State University Press. Abstracts of Doctors' Dissertations, number 16:253–265.
- YOUNG, R.A. 1945. Bamboos for American horticulture (I). Natl. Hort. Mag. 24:195–196. YOUNG, R.A. and J.R. HAUN. 1961. Bamboo in the United States: descriptions, culture, and utilization. United States Dept. Agric., Crops Res. Div., Agric. Handbook No. 193, Washington, D.C.
- ZHANG, W.P. and L.G. CLARK. 2000. Phylogeny and classification of the Bambusoideae (Poaceae). In: Jacobs, S.W.L., and J. Everetts, eds. Grasses: systematics and evolution. Pp. 35–42. CSIRO, Melbourne.

